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# Native-alien populations—an apparent oxymoron that requires specific conservation attention

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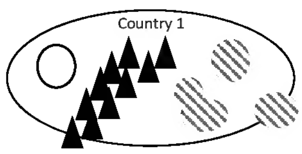
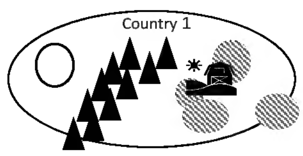
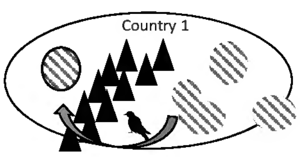
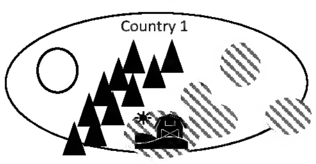
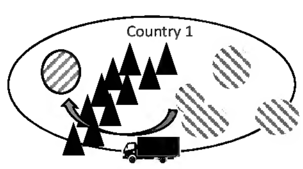
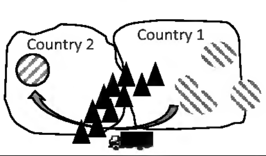
## Abstract
Many countries define nativity at a country-level—taxa are categorised as either alien species or native species. However, there are often substantial within-country biogeographical barriers and so a taxon can be native and alien to different parts of the same country. Here, we use the term 'native-alien populations' as a short-hand for populations that result from the human-mediated dispersal of individuals of a species beyond a biogeographical barrier to a point beyond that species' native range, but that is still within the same political entity as parts of the species' native range. Based on these criteria, we consider native-alien populations to be biological invasions. However, we argue that, in comparison to other alien populations, native-alien populations: 1) are likely to be closer geographically to their native range; 2) are likely to be phylogenetically and ecologically more similar to native species in their introduced range; and 3) options to control their introduction or manage them will likely be more limited. We argue this means native-alien populations tend to differ from other alien populations in the likelihood of invasion, the types of impacts they have, and in how they can be most effectively managed. We also argue that native-alien populations are similarly a distinct phenomenon from native populations that are increasing in abundance or range extent. And note that native-alien populations are expected to be particularly common in large, ecologically diverse countries with disjunct biomes and ecoregions. Reporting, monitoring, regulating and managing native-alien populations will, we believe, become an increasingly important component of managing global change.

## Keywords
Alien species, biogeographical barriers, dispersal, human agency, native species, terminology

## Introduction

The regulation and management of biological invasions often focus on the species-level [e.g. the current Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services thematic assessment is on 'invasive alien species' (IPBES 2019)]; however, biological invasions are fundamentally a population-level phenomenon (Essl et al. 2020). A species might be native to a part of a country (or part of another political entity at which level management decisions are made), but individuals and/or propagules can be moved by humans to another part of the country or political entity (e.g. provinces, states etc.) where the species is not native (Spear and Chown 2009). Therefore, a species can have both native and alien populations within the same country (Fig. 1 and Table 1). For example, some plants that are native to Eastern Australia have been transported by humans and have become invasive in Western Australia (e.g. *Pittosporum undulatum*) and vice versa (e.g. *Acacia saligna*) (Head and Muir 2004). The presence of the Nullabor Plain, as a biogeographic barrier separating Eastern and

| Phenomenon | | Description | Examples |
|---|---|---|---|
| **~Stable Native range** |  | Species X had three native populations.<br><br>There has been no significant recent changes in the number, extent or abundance of populations. | For many species endemic to South Africa, the Cape fold mountains separate potentially suitable ranges from currently occupied native ranges (e.g., Proteaceae species, Manning 2018). |
| **Human-mediated increase in native abundance** |  | Recent human-induced environmental change has led to an increase in the abundance of Species X within its original native range | The rock lobster (*Jasus lalandii*) has increased in abundance in its native range in the Western Cape province because an increase in nutrient levels has led to an increase in food availability (Van Zyl et al. 1998) |
| **Natural range expansion** |  | Species X naturally spread forming a new native population | The Murex snail (*Acanthinucella spirata*) evolved morphologically in the Pleistocene and consequently expanded its range on the coast of California in the United States of America (Hellberg et al. 2001). |
| **Range expansion in response to human-induced environmental change** |  | Human modification of the environment meant that a new range became suitable for colonisation by Species X, which naturally spread to form a new native population | Birds and butterflies in Europe have shifted their ranges due to climate change (Devictor et al. 2012) |
| **Biological invasion (within-country)** |  | Species X was dispersed by humans within Country 1 forming a new alien population<br><br>In this paper we refer to native species with alien populations as native-alien populations. | The guttural toad (*Sclerophrys gutturalis*) has been introduced from its native range in KwaZulu-Natal province in South Africa and established a native-alien population in the Western Cape province where it is not native (Measey et al. 2017) |
| **Biological invasion (between countries)** |  | Species X was dispersed by humans from Country 1 to Country 2 forming a new alien population.<br><br>Both the species and the population can be regarded as alien to the whole of Country 2. | 240 tree species alien to South Africa have established populations (Richardson et al. 2020) |

Native range; Increased abundance in native range; Alien range; Mountain; Unoccupied range

Human assisted dispersal; Natural dispersal; Human induced environmental change

**Figure 1.** How the concept of native-alien populations differs from other instances of changes in range/abundance. These are idealised versions and are not mutually exclusive. See Table 1 for a summary of how the different phenomena differ in terms of processes and properties.

**Table 1.** The properties of native-alien populations and other related phenomena. The presented processes and properties are based on Essl et al. (2019) and Ogden et al. (2019). The situation for a stable native range is not shown as it forms the baseline against which the other phenomena are compared.

| Phenomenon | Biogeographic barrier | Survival and reproduction | Distance from native range | Range expansion within political entities |
|---|---|---|---|---|
| Human-mediated increase in native abundance | No barrier crossed | There is likely to have been an increase in survival or reproduction | Within native range | No range expansion |
| Natural range expansion | Biogeographic barrier crossed naturally | Rates need not have changed in most of the native range, but some increase in neighbouring areas | Within natural dispersal distance of native range | Within or between political entities |
| Range expansion in response to human-induced environmental change | Human-induced changes might have weakened biogeographic barriers | There is an increase in survival and reproduction in neighbouring areas | Within natural dispersal distance of native range | Within or between political entities |
| Biological invasion (within-country) | Biogeographic barrier crossed by human agency | Individuals will not always survive and reproduce in the new range, but could if the environment is suitable | Further than natural dispersal distance from native range | Within political entity |
| Biological invasion (between countries) | Biogeographic barrier crossed by human agency | Individuals will not always survive and reproduce in the new range, but could if the environment is suitable | Further than natural dispersal distance from native range | Between political entities |

Western Australia, means that such cases are relatively clear-cut; however, in other cases, whether populations should be considered as native or alien is uncertain. For example, following the introduction of the American bullfrog (*Lithobates catesbeianus*) from the eastern United States of America (USA) to some of the country's western states, there was confusion over the species' status—populations were classified as native by some researchers and alien by others (Guo and Ricklefs 2010). Confusion over how such introductions should be classified is partly the result of uncertainties in defining native ranges (Webber and Scott 2012; Essl et al. 2018; Pereyra 2019), partly as the phenomenon has not been clearly defined, and partly as biosecurity is implemented primarily at a country's borders and not always within a country.

As for all introductions, within-country introductions can provide socio-economic benefits (Maciejewski and Kerley 2014). Moreover, assisted migration within a country might also be essential for species' survival (Hunter 2007). However, as with all types of biological invasions, such introductions can pose significant problems. In the USA, rainbow trout (*Oncorhynchus mykiss*), which is native to eastern USA, has been introduced to western USA where it hybridises with California golden trout (*O. mykiss aguabonita*) and Paiute cutthroat trout (*O. clarki seleniris*) (Lockwood et al. 2013). When the California golden trout and Paiute cutthroat trout hybridise with rainbow trout, the offspring are fertile and can mate with either parental population. This has led to introgression which threatens the genetic integrity of these rare native taxa (Moyle 2002) and has led

to declines in their populations (Lockwood et al. 2013). In South Africa, the antelope *Damaliscus pygargus phillipsi* (blesbok) is native to much of the country, but not to the Western Cape province. Blesbok were introduced and established alien populations in the Western Cape, hybridising with the endemic bontebok (*D. pygargus pygargus*) (van Wyk et al. 2017). This hybridisation has occurred between non-admixed bontebok/non-admixed blesbok and hybrids, but no F1 individuals have been identified. Only through concerted and intensive interventions was the extinction of the bontebok prevented.

Alien species that have been introduced from one country to another receive the majority of research attention and biological invasion frameworks are often developed with such introductions in mind. In contrast, those that have established alien populations within countries to which they are native have received relatively little research attention (Vitule et al. 2019). For example, in the Global Register of Introduced and Invasive Species (GRIIS), only a few countries (including Spain and the USA) report such populations—the majority of countries (including Brazil and South Africa) do not (http://www.griis.org: Data accessed 20 July 2021). Moreover, in the USA, while the presence of alien populations of species that are native to the USA have been recognised, the severity of their potential impacts has been neglected (Guo and Ricklefs 2010). Globally, established alien populations of species that are native at the country-level are often ignored in analyses and, consequently, the scope of biological invasions and their impacts are underestimated and management actions could be misinformed (Vitule et al. 2019). This gap in research is partly because most of the monitoring, reporting, and management of biological invasions is performed at national or larger administrative levels [e.g. through national-level reports to the Convention on Biological Diversity (CBD)]. While national and international mechanisms seek to manage the movement of species between countries (such as CITES), instruments that control the purposeful or inadvertent human-mediated within-country movement of species are, in general, lacking, and in countries where such regulations do exist the legislation is often poorly enforced (Measey and Davies 2011).

In this perspective piece we: 1) define this phenomenon; 2) contrast it with other forms of range changes; 3) discuss expectations of how this phenomenon is likely to differ from other biological invasions; 4) identify situations where it is most likely to occur; and 5) discuss the management implications.

## A proposed definition

The presence of biogeographical barriers means that some species occur in the same place at the same time (sympatric speciation), while other groups of organisms are separated by a physical or geographic barrier (allopatric speciation) (Orr and Smith 1998). Sympatric speciation is defined as evolution of intrinsic barriers to gene flow in the absence of extrinsic barriers, while allopatric speciation is the evolution of intrinsic barriers to gene flow in the presence of extrinsic barriers (Orr and Smith 1998). An

**Box 1.** Terms used to describe native-alien populations.

The ISI Web of Knowledge and Google Scholar were searched between May and June 2020 using the following search strings: "Intra-country established alien species", "Intracontinental exotics", "within-country aliens", "within-country movement of native species", "native-alien populations", "extralimital species", "alien natives", "domestic exotics", "native alien species". Note that 'native invaders' (sensu Simberloff 2011) are distinct from 'native-alien populations', as native invaders become 'invasive' (increase in abundance or extent) within their native range (see 'Human-mediated increase in native abundance' and 'Range expansion in response to human-induced environmental change' in Table 1). The following discrete terms were found.

**Domestic exotics:** Species that form invasive populations outside of their natural distribution, but within the borders of the same nation (Guo and Ricklefs 2010). [6 hits]

**Extralimital species:** Indigenous species translocated or intended to be translocated to a place outside its natural distribution range, but excluding an indigenous species that has extended its natural distribution range by natural means of migration or dispersal without human intervention (Spear and Chown 2009). [> 20 hits]

**Home-grown exotic:** Species that form invasive populations outside of their natural distribution, but within the borders of the same nation (Cox 1999). [1 hit]

**Intra-country established alien species:** Species that are introduced and establish amongst regions or in a novel region within the same country (Vitule et al. 2019). [1 hit]

**Native-alien species:** Species native to some areas of a country or territory, but introduced by humans into places outside of their natural range of distribution in that country, where they become established and disperse (Pagad et al. 2018). [1 hit]

While the term 'extralimital species' was the most common, we prefer 'native-alien' as it is explicit regarding the population's status at political and biogeographic levels and as it is currently used in the Global Register of Introduced and Invasive Species (Pagad et al. 2018). However, we adapted the term (to "native-alien population") to reflect that invasions are a population level phenomenon. The global biodiversity standard, Darwin Core, currently allows for each record to be classified as either native or introduced to that site according to the term 'establishmentMeans' as: introducedAssistedColonisation, vagrant and uncertain (https://dwc.tdwg.org/em/; Groom et al. 2019). Native-alien populations would, therefore, be classified as introduced, but this will not separate native-alien populations from other alien populations, unless linked to additional information on national status, it will be important that this is clarified in any future revisions to the term.

alien species is defined as an organism whose presence in a region is due to human-mediated dispersal (i.e. direct human agency or substantial indirect human agency) across a biogeographic barrier to a site where the species has not recently naturally occurred (Essl et al. 2018). Though here we note that the use of the term 'species' is a misnomer, as biological invasions and evolution operate at the population-level. Definitions differ as to what constitutes an invasive population, but it is generally taken to be alien organisms that survive and spread from sites of introduction to form self-sustaining populations (Blackburn et al. 2011), that, in some definitions, may cause negative impacts (e.g. CBD 2002). Regardless of the precise definition, the relevant biogeographic barriers that separate native ranges from (potential) alien ranges need not coincide with political boundaries. These biogeographical barriers include abiotic barriers, such as mountain ranges and changes in climatic conditions, and biotic barriers, such as the absence of key interacting species. As a consequence, if individuals are moved by humans within a country to which they are native and this results in the establishment of a population beyond the species' native range, a species can technically be both alien and native in the same country (Spear and Chown 2009). Hereafter,

we refer to such populations using the short-hand 'native-alien populations' (see Box 1 for other terms used). This term might seem oxymoronic, but 'native' refers to the status of the population in a political entity (e.g. a country), while 'alien' refers to biogeographical status. This means that, in the context of alien-native populations, the terms alien and native can refer to status at different spatial scales. As with alien populations introduced from other countries, the status of a native-alien population can be classified as casual, established or invasive [as per the recently adopted Darwin Core term 'dwc:degreeOfEstablishment' (see Groom et al. 2019)]. To facilitate the implementation of the term native-alien populations, we have developed a protocol, based on the definition (manuscript in preparation). This means there is a process both to circumscribe the phenomenon and to confirm instances, with a clear link through to the causes and consequences (Latombe et al. 2019).

We, therefore, define a native-alien population as a population that is: (1) within a country to which the species is native, (2) founded by individuals moved by direct human agency [or substantial indirect human agency, see Essl et al. (2018)], (3) over a biogeographical barrier and (4) to an area beyond the species' native range. We believe the use of this term is justified because, while native-alien populations are a subset of alien populations, their properties are likely to differ from other alien populations and these differences are likely to have consequences for invasion success, impacts, management and regulation (Table 1). The development of a clearly-defined term that distinguishes these populations from other range changes and alien populations will be beneficial, as it will enable the development of conceptual frameworks that can be used to classify these populations and so reduce uncertainties in invasion science (Heger et al. 2021). Various terms are currently in use for the native-alien population phenomenon (Box 1) and, therefore, we encourage one terminology be used by everyone globally.

## Native-alien populations differ from other forms of range change

The capability of an organism to colonise suitable, but unoccupied habitats or environments through natural dispersal depends on its dispersal traits. The dispersal of a species is facilitated by three processes: (1) natural processes (evolution and natural environmental changes); (2) human-mediated dispersal (including biological invasions); and (3) human-induced environmental change (i.e. land-use change, human-disturbance, human-mediated climate change) (Table 1). Evolutionary changes that could facilitate range expansion include shifts in host range or the development of resistance to herbicides. As an example, the murex snail (*Acanthinucella spirata*) evolved morphologically in response to climatic changes in the Pleistocene and consequently expanded its range on the coast of California in USA (Hellberg et al. 2001). Similarly, native species can shift their ranges by responding to natural environmental changes. Natural range expansion and contraction has been reported in a number of taxa in response to natural climatic variation, where species ranges expand into cooler regions

when the climate warms and then contract again during cooling periods (Parmesan and Yohe 2003). Examples of this phenomenon have been reported for marine fish, limpets, barnacles, and zooplankton in the United Kingdom (Southward et al. 1995) and butterflies in Finland and Sweden (Henriksen and Kreutzer 1982; Parmesan et al. 1999). These range expansions and contractions are infrequent and usually occur adjacent to the native range. Human-assisted dispersal can occur through the intentional or unintentional transport of propagules by humans, either within or between countries, to different biogeographical regions. For example, *Sclerophrys gutturalis* (Guttural toad), which is native to South Africa, has been introduced unintentionally by humans to areas outside its native range within South Africa (Measey et al. 2017), while 240 tree species, alien to South Africa, have been introduced from Australia (Richardson et al. 2020). Species can also spread into new areas by tracking human-induced environmental changes, such as climate change or the removal of predators (Essl et al. 2019). For example, birds and butterflies in Europe have shifted their ranges due to climate change (Devictor et al. 2012). Alternatively, human-modification of the environment can facilitate an increase in the abundance of species within their native ranges. For example, the rock lobster (*Jasus lalandii*) has increased in abundance in its native range in the Western Cape province of South Africa because an increase in nutrient levels has led to an increase in food availability (Van Zyl et al. 1998). Human assisted dispersal of organisms to new regions, whether within or between countries, is likely to result in reproductive isolation as the newly-formed native-alien or alien population could be isolated from its native range by a biogeographical barrier and would result in biotic homogenisation at the species-level. In contrast, changes to the abundance and/or range of organisms within or adjacent to their native range, due to natural processes or human-induced environmental changes, are unlikely to result in reproductive isolation, but will often also lead to biotic homogenisation (McKinney 2005).

The three processes that facilitate dispersal (natural processes, human agency and human-induced environmental change) can act synergistically to ensure that a species reaches suitable, but unoccupied habitat (Essl et al. 2019). For example, species can be moved by humans from their native range to new areas that were previously not suitable for establishment, but are now suitable due to human-induced environmental changes. In addition, many synanthropic species (e.g. the house mouse) would be expected to show increases in abundance and extent of populations within their native ranges, i.e. as a result of human modifications to the environment, they might also have formed alien populations in countries to which they are alien and in countries to which they are native to a part of. The three processes described above result in a number of distinct phenomena that will tend to differ in key features (Fig. 1, Table 1). Here, we focus on why native-alien populations will likely differ from alien populations introduced from other countries in several important ways and, as a consequence, the likelihood of invasion and the types and magnitude of impact these phenomena have are likely to differ, noting that native-alien populations will only occur under the conditions defined above.

Native-alien populations are expected to be physically much closer to their native range than alien populations introduced from other countries, with the geographic distance roughly an order of magnitude different (Fig. 2; $t = 15.6$, $df = 64.4$, $P < 0.001$). Given the shorter geographical distances, it is likely that native-alien populations will differ from alien populations introduced from other countries in key properties of dispersal, including propagule pressure, genetic diversity (Vilatersana et al. 2016), potential for simultaneous movement of co-evolved species, selectivity of what is moved, and the duration of dispersal opportunities (Wilson et al. 2009). Such differences may lead to quantitative and qualitative differences in the probabilities of establishment and invasion and in the types of impact that are likely to occur. For example, the relatively short distance between these native-alien populations and their native range, means that propagule pressure [i.e. encompassing the number of individuals introduced and the number of introduction events for any particular species (Lockwood et al. 2009)] will likely be higher than for alien populations introduced from other countries. In addition, the higher the number of introduction events the greater the chance that propagules come from a wide variety of sources and the higher the potential genetic diversity. Therefore, genetic diversity is potentially higher for native-alien populations than for alien populations introduced from other countries (Vilatersana et al. 2016). These differences will have consequences for invasion potential (Bossdorf et al. 2005; Roman and Darling 2007) because, if propagule pressure is low, the entire genetic diversity of the species is unlikely to be present in the introduced individuals (Wilson et al. 2009) and this could

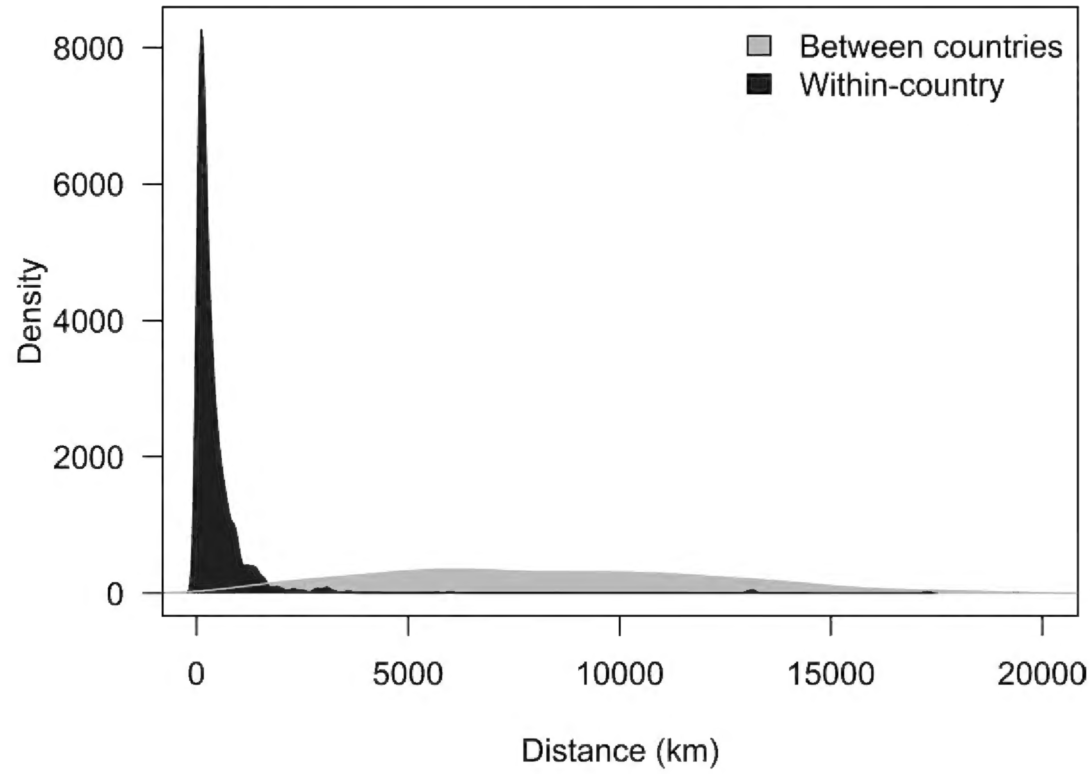



**Figure 2.** Density plot showing the distance between any two random points within a country and between two random points in different countries ($t = 15.6$, $df = 64.4$, $P < 0.001$). The distance between random points within a country ('within-country') represents the distance between native-alien populations and their native range, while the distance between random points in different countries ('between countries') represents the distance between alien populations introduced from other countries and their native range. See Suppl. material 1 for full methods.

result in genetic bottlenecks that reduce the chances of survival (Excoffier et al. 2009). In contrast, high propagule pressure is likely to result in a large proportion of the total genetic diversity of a species being present in the introduced population, increasing the chances of species survival and invasion success (Roman 2006).

**Table 2.** Number of plant species with native-alien populations and alien populations introduced from other countries that are in the same genus and family as native species in their alien range, at local and national levels. Local level is the Garden Route National Park in South Africa (Baard and Kraaij 2019), while the national level is the whole of South Africa, excluding islands (SANBI 2019). These data were analysed using Chi-square tests and Fisher's exact tests (in instances where there were expected values of less than 4, see Crawley 2007). See Suppl. material 2 for full methods.

| **a) Local (the Garden Route National Park)** | | | |
|---|---|---|---|
| | **Native-alien populations** | **Alien to the whole of South Africa** | **Analysis** |
| Number of species with congeners present | 14 (93%) | 10 (10%) | P = < 0.001, Fisher's exact test |
| Number of species with confamilials present | 15 (100%) | 72 (72%) | P = 0.020, Fisher's exact test |
| Number of species | 15 | 100 | |
| **b) National (South Africa)** | | | |
| | **Native-alien populations** | **Alien to the whole of South Africa** | **Analysis** |
| Number of species with congeners present | 71 (95%) | 900 (23%) | $\chi^2$ = 201.25, df = 1, P = < 0.001 |
| Number of species with confamilials present | 75 (100%) | 2230 (57%) | $\chi^2$ = 56.008, df = 1, P = < 0.001 |
| Number of species | 75 | 3912 | |

In the context of invasion science, alien organisms are expected to be ecologically novel in their introduced range (i.e. evolutionarily and ecologically different from native species) (Saul and Jeschke 2015). However, as there is a relatively short geographical distance between native-alien populations and their native range (Fig. 2), there tends to be a greater number of closely-related taxa in the introduced range of native-alien populations in comparison to alien populations introduced from other countries (see Table 2) and this means that native-alien populations are likely to be less phylogenetically and ecologically distinct from native populations in their alien range (Saul and Jeschke 2015; Essl et al. 2019). This will have consequences for the probability of invasion [cf. Darwin's Naturalisation Hypothesis (Darwin 1859; Daehler 2001)] and the types of impact. As there has been less time for differentiation or reproductive isolation, native-alien populations might be less likely to possess traits that are new to the alien range (e.g. novel weapons), but more likely to occupy similar niches to those occupied by native populations (Callaway and Ridenour 2004). Consequently, native-alien populations are, in general, more likely to experience higher levels of competition (Gilbert and Levine 2013) and natural enemies (Enders et al. 2020) in their introduced range, but are also more likely to be suited to the abiotic conditions (e.g. climate), and suitable mutualists are more likely to be present. Native-alien popula-

tions are also more likely to hybridise with closely-related native populations (Bossdorf et al. 2005; Roman and Darling 2007; and examples of rainbow trout introductions in USA and blesbok introductions in South Africa, discussed above).

## Which conditions give rise to native-alien populations?

Native-alien populations can be found in any nation where biogeographic barriers prevent organisms from dispersing to suitable, but unoccupied ranges. However, large countries are, generally, more environmentally heterogeneous than smaller countries (Fig. 3 and Suppl. material 3: Fig. S1b). Large countries tend to have more biomes (Fig. 3a) and more ecoregions (Suppl. material 3: Fig. S1a) than smaller countries; and have more biomes (Fig. 3b) and ecoregions (Suppl. material 3: Fig. S1b) that are non-contiguous. Therefore, while country size is an imprecise proxy of environmental heterogeneity and the presence of biogeographical barriers, native-alien populations are likely to be more common in large countries than small countries. We note that native-alien populations are likely to be particularly prevalent in countries like Russia, the USA, and India, because they have a relatively high number of biomes and ecoregions, and a high number of non-contiguous biomes and ecoregions (Fig. 3; Suppl. material 3: Fig. S1). We tried to explore this issue using a global dataset of bird introductions, but even for this well-studied group, the data quality was not sufficiently reliable (see Suppl. material 3).

We also hypothesised that taxa that are both poor dispersers, and that are likely to be moved by humans are most likely to form native-alien populations. These are taxa for which dispersal distances are short enough that the native range can be restricted to one part of a country, and suitable alien range can only be reached with substantial assistance from humans. However, we did not find a suitable dataset to test this. Testing

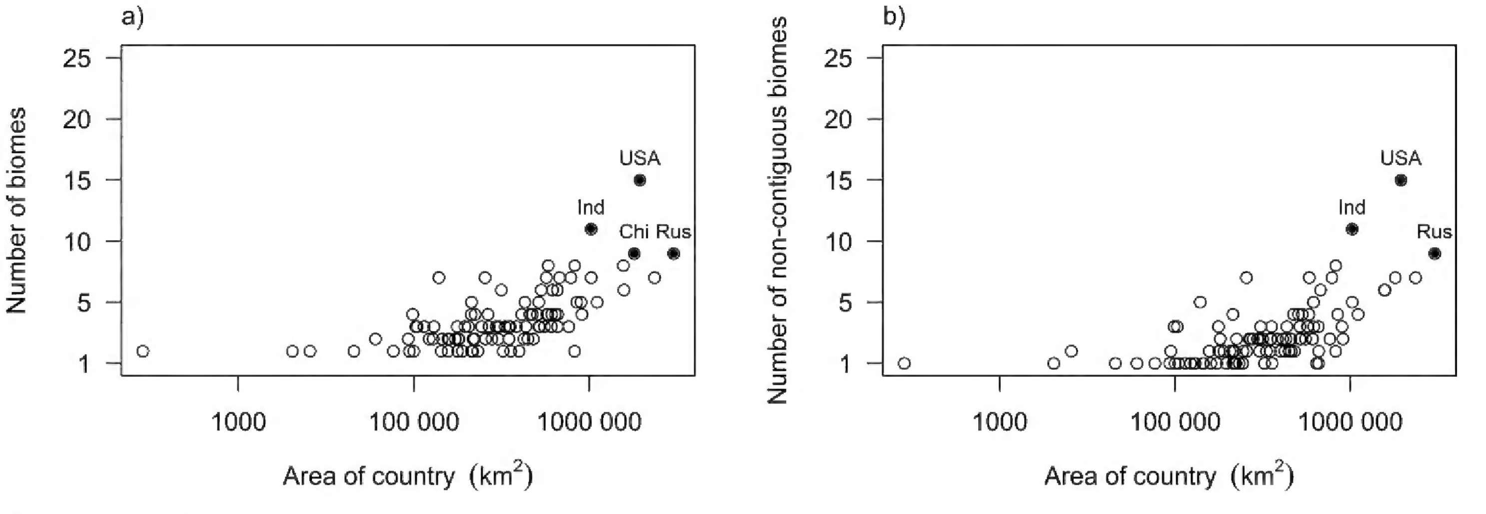



**Figure 3.** The relationship between country size and a) the number of biomes in the country (Generalised linear model: t = 19.20, df = 106, P < 0.001); and b) the number of biomes with non-contiguous patches (Generalised linear model: t = 24.45, df = 106, P < 0.001). A similar pattern is evident for ecoregions (Suppl. material 3: Fig. S1). See Suppl. material 3 for full methods. USA: United States of America, Ind: India, Chi: China, Rus: Russia.

which species-level traits are more likely to result in native-alien populations will require some careful analyses, but will be important to better understand the phenomenon and, arguably, might reveal differences in the propensity of taxa to become invasive.

## Management implications

A country's conservation or biodiversity management goals play a crucial role in determining whether a population is classified as native or alien. The focus of management goals has consequences because if too much attention is paid to preventing new introductions from other countries, then within-country invasions could be missed. For example, in USA, the impacts of native-alien populations have been realised, but the management response has been delayed (Guo and Ricklefs 2010), while the impact of alien populations introduced from other countries have been given a full management response. Therefore, native-alien populations are treated and managed differently by different countries. However, there may also be differential management across lower political levels (e.g. provinces, states) and, consequently, native-alien populations could be managed in different ways (as native or alien) in different parts of the same country. However, such differential management may make sense in some cases, for example, in cases where provinces or states vary in size or vary in their biological diversity, native-alien populations may be more prominent in some provinces or states than others. National legislation can be used to guide the management of native-alien populations. For example, in South Africa, native species, such as *Sclerophrys gutturalis* and *Hyperolius marmoratus* (both amphibians), are listed under the National Environmental Management: Biodiversity Act (NEMBA) as invasive species that require compulsory control in the Western Cape province, but are not listed as invasive species in their native ranges in the Limpopo, Mpumalanga, and KwaZulu-Natal provinces (Department of Forestry Fishery and the Environment 2013; Measey et al. 2017). As these native-alien populations can result in invasions at provincial or state levels and cause negative impacts on native populations where introduced, sub-national regulation might be preferable. For example, an analysis of native and alien plant distributions by Rouget et al. (2015) supported biome-level strategies for the control of alien plant species in South Africa. There is, thus, a need for a careful alignment of management and policy between different geographic and political scales from national to local. However, while it might make more ecological sense to regulate and manage native-alien populations, based on biogeography, this is often impractical both due to bureaucracy and biology. Funds and management are often administered according to political boundaries and which biogeographic breaks are important might be highly context-specific.

Classifying the introduction status of populations relies largely on knowing where the native range is within a country. This is expected to be easy for taxa, such as large mammals, that have been monitored and tracked over time (Skinner and Chimimba 2005) and for which data on human-mediated transportation exist. Conversely, it will

be very difficult for other taxa, such as microbes, for which the native range is not well circumscribed and that have been moved unintentionally by humans using vectors and pathways that are poorly understood. For example, it is difficult to identify the location of the native range of marine species due to a lack of surveys across a number of marine environments, a lack of taxonomic expertise, the use of different terms in marine invasion science and challenges with taxonomic resolution at a global scale for a number of species (Robinson et al. 2005; Mead et al. 2011; Robinson et al. 2016). Native ranges are likely to expand and contract naturally and, in some instances, species might be introduced by human action into areas where they have historically occurred. This creates problems when identifying native-alien populations as these shifts increase uncertainty when describing the native range.

## Conclusion and recommendations

We have argued here that native-alien populations will likely differ from other biological invasions and other forms of range shifts in terms of geographic, evolutionary, and ecological characteristics. Native-alien populations can cause significant and often specific negative impacts [through hybridisation in particular, for example, van Wyk et al. (2017) and Lockwood et al. (2013)]. We recommend a standardised approach to be used to compile lists of native-alien populations, for example, that taken by the Global Register of Introduced and Invasive Species (Pagad et al. 2018). Management and regulation should also ideally follow relevant biogeographic barriers or at least operate at the political level most relevant for a particular group of taxa, but this is often impractical at present. To conclude, while we recognise that the phenomenon of native-alien populations is an artefact of political boundaries, it has inherent regulatory implications and so the phenomenon must be increasingly and explicitly included in conservation predictions, planning, and management so that these populations are correctly classified, included in alien species inventories, and managed as biological invasions.

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## Data resources

Data for this study are available on request from the authors.

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## Supplementary material 1

**File S1**

Authors: Takalani Nelufule, Mark P. Robertson, John R. U. Wilson, Katelyn T. Faulkner

Data type: Methods (docx. file)

Explanation note: Methods for the simulation that illustrates that native-alien populations are likely to be closer geographically to their native range than populations introduced from other countries.



Link: https://doi.org/10.3897/neobiota.74.81671.suppl1

## Supplementary material 2

**File S2**

Authors: Takalani Nelufule, Mark P. Robertson, John R. U. Wilson, Katelyn T. Faulkner

Data type: Methods (docx. file)

Explanation note: Method for determining whether native-alien populations tend to have a greater number of closely related taxa (congeneric and confamilial species) in their introduced range than alien populations introduced from other countries..



Link: https://doi.org/10.3897/neobiota.74.81671.suppl2

## Supplementary material 3

**File S3**

Authors: Takalani Nelufule, Mark P. Robertson, John R. U. Wilson, Katelyn T. Faulkner

Data type: Methods (docx. file)

Explanation note: Method for testing whether native-alien populations are particularly prevalent in large, ecologically diverse countries.



Link: https://doi.org/10.3897/neobiota.74.81671.suppl3